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From: Sbornik "Opyt izucheniya regulyatsii
fiziologicheskikh funktsii v estestvennykh
uslovyakh sushchestvovaniya organizmov,"
Vol. 6:35-40. 1963.

A. F. Davydov

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(O rezhime myshechnoi deyatel'nosti severnykh
olenei pri dobyvanii korma iz-pod snega)

Translated from Russian
IPST Cat. No. 1860

Published Pursuant to an Agreement with
The U.S. Department of the Interior and
The National Science Foundation, Washington, D.C., by the
Israel Program for Scientific Translations
Jerusalem 1967

Pam: 599.735.3:(*50) DAV

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ON THE PROCESSES OF MUSCULAR ACTIVITY IN REINDEER DURING PROCUREMENT OF FEEDS FROM UNDER THE SNOW

(O rezhime myshechnoi deyatel'nosti severnykh olenei pri dobyvanii korma iz-pod snega)

A.F. DAVYDOV
The Laboratory of Ecological Physiology (Director—Professor A. D. Slonim),
The Pavlov Institute of the Academy of Sciences of the USSR
(AN SSSR) and the Institute of Agriculture of the Far North
of the Ministry of Agriculture, RSFSR (Director—N. O. D'yachenko)

The feeding of hoofed mammals in winter has been mainly studied in its qualitative and quantitative aspects. Works are also available on the peculiar features of adaptation exhibited by wild and domestic ungulates in foraging for food under the snow (Davydova and Stepanov, 1936; Igoshina and Florovskaya, 1939; Odintsov and Chelyshev, 1941; Formozov, 1946; Semenov-Tyan'shanskii, 1948; Mertts, 1953; Nasimovich, 1955; Sablina, 1955, and others). It has been established that most ungulates possess the capacity to secure food from under the snow with their forelimbs, this depending more or less on the depth of the snowcover.

There are no published data relating to the modes of muscular activity of ungulates during foraging and grazing. It is therefore informative to study animals whose winter diet contains practically no shrubby or woody vegetation, and which derive their food from under the snow (reindeer, sheep, bighorn sheep, Yakutsk horse). Particularly important is how these animals maintain a prolonged capacity for exertion, without rapid fatigue, when engaged in foraging in the snow under extremely difficult conditions (in deep and loose snow, or in hard-crusted, deep snowcover).

The numerous investigations of the physiological mechanisms for maintaining prolonged work-capacity have been almost exclusively carried out on humans.

Slonim (1957) maintains that, in animals, high capacity for work exertion without rapid muscle fatigue is due to alternation of different forms of muscular activity (vertical and horizontal motions in monkeys, digging and gnawing in rodents). The basis for maintaining prolonged capacity to do work is the phenomenon of "active rest" first described in man by Sechenov (1903).

Investigations carried out on reindeer may prove of great interest in the study of active rest. The motor activity in reindeer shows considerable quantitative variation in accordance with the depth and physicomechanical properties of the snowcover (Davydov, 1958). Supplementary

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observations on the Kola Peninsula were carried out on the processes of muscular activity of domestic reindeer engaged in digging up snow of varying depth, density and hardness.

To study the amount of labor consumed in digging, the following methods of timing and measuring were employed. During 10 minutes' snow-digging by an adult deer (buck) at one place, all digging motions with the left and the right limb respectively were counted in turn, as were the number of intervals between the digging periods. The speed of digging motions was timed with a stopwatch. Before and after pasturing a herd of deer on similar pastures with a similar snowcover, a selected group of deer were weighed (usually every 10 to 15 days). The depth of the snowcover was measured with a surveyor's rod, its hardness with the durometer proposed by Popov (1956), and snow density with snow-scales.

The investigations were made during various pasturing seasons. Pasturage in a forest (pine—lichen woods) took place in mid-winter when the snow was deep and loose, and at the end of winter with the development of frozen snowcrust. Pasturage in mountainous lichen—shrub tundra was carried out in mid-winter, when the snowcover was thin but quite dense, and at the end of winter or in early spring when thawed patches in the snow appeared. Altogether 68 observations were made, 45 under conditions of loose, deep snow, and 23 in dense, hard tundra snow.

Results

Reindeer on the Kola Peninsula feed in winter on forest pastures and in mountain tundras. These two types of pastures have snowcovers differing distinctly in their depth and physicomechanical properties (Table 1).

TABLE 1. Character of snowcover at pastures

	Forest pastures		Mountain tundras	
	March	April (frozen snow-crust)	March	April
Depth (cm)	50—60	60—70	36—68	17—44
Density (g/cm^3) . . .	0.18—0.23	0.20—0.25	0.32—0.34	0.31—0.44
Hardness (kg/cm^2) . . .	< 0.3	> 0.3	> 0.3	$\geqslant 0.3$

Snow surfaces having a degree of hardness exceeding 0.3 kg/cm^2, typical of mountain-tundra pastures, easily support moving adult deer. Only a thaw of several days' duration softens such a snowcover (to a hardness below 0.3 kg/cm^2), so that deer may fall through it, even though the snow density may reach 0.44 g/cm^3.

The nature of the snowcover seems to be one of the main factors affecting the motor activity of reindeer when digging (Davydov, 1958).

The number of digging motions increases with increased depth of the loose snow, while ambulatory movements in the pasture diminish. In mountain tundra the snow is unevenly distributed; here deer look for and dig up food on sections with the thinnest snowcover. This explains why ambulatory movements during grazing on mountain tundra are more pronounced than on forest pastures. Under both conditions, the total time spent in muscular activity for digging and moving about is about 2 hours in a 24-hour period: on mountain tundra, up to 40 minutes for digging and 80 minutes for ambulation; on forest pastures, the corresponding times are 50 and 60 minutes respectively.

The number of motions per 24 hours digging up loose snow on forest pastures differs from that when hard snow is dug up on mountain tundra. There are also differences in the speed of digging, in the frequency of alternating the limbs, and in the number of digging motions per 10 minutes (Table 2).

TABLE 2. Characteristics of digging activity of deer in various snowcovers (average values for 10-minute periods)

	Forest pastures			Mountain tundras
	March	April (damp)	April (frozen snowcrust)	
Number of observations	37	8	9	14
Total digging motions	138	140	155	155
Digging motions with left limb	68	81	80	49
Maximum number of digging motions with one limb (without switching to the other limb). . .	38	41	42	53
Number of intervals in digging (spent in eating) .	22.3	22.7	20.5	24.6
Ratio of time spent in digging to that spent in eating	1:6.2	1:6.1	1:5.8	1:7.6

The average number of digging motions per 10 minutes is somewhat smaller (by 12.4%) under conditions of loose snow on forest pastures than in hard, dense snow on mountain tundras. The formation of a hard crust on the surface of soft snow in forests led to an increase in the number of digging motions. The increased hardness of the snow under the frozen snowcrust on forest pastures resulted not only in the exertion of greater force in breaking the crust, but also in an increased average number of motions for one digging period from 6.4 to 7.7 (an increase of 20%). With higher resistance of the snow, the speed of digging motions changed: on mountain tundra pasturage, the speed was one stroke per 0.40—0.45 seconds, and on forest pasture, 0.56—0.60 seconds. With frozen snowcrust on forest pastures (hardness of snow 0.3 kg/cm^2 or more), the first 2 or 3 digging motions were performed at the rate of one stroke per 0.30—0.35 seconds. After breaking the snowcrust deer continued digging at the speed of one stroke per 0.56—0.60 seconds.

Normally, while digging at one hole for 10 minutes, a deer stopped digging on the average 20 to 24 times in order to eat. The number of digging strokes performed by one limb was subject to variation within a wide range: from 2 to 18 in forest tracts, and from 2 to 22 when digging up dense, hard snow. Without switching to the other limb, but with intervals for eating, deer could perform on the average 38 motions (range: from 18 to 64) in loose snow 60 to 70 cm deep. In hard tundra snow, deer performed on the average 53 digging motions (range: from 33 to 103). During prolonged digging at the same place, the limb was held frequently in a semi-bent position, with the entire weight of the front part of the body on the other limb. Digging up deep, loose snow was carried out practically to the same extent with both limbs, whereas hard, dense snow was dug predominantly with the right limb.

On forest pastures the average duration of one feeding period became shorter as the depth of the snowcover increased: from 147 minutes in snow 20—25 cm deep (December), to 92 minutes when the snow reached a depth of 60—70 cm (March—April). However, the total number of feedings per 24 hours rose from 4 to 5 in early winter to 6 to 8 at winter's end. In still harsher conditions (frozen snowcrust on forest pastures covered with deep snow), the average duration of one feeding period in a group of deer decreased to 83 minutes, with a correspondingly longer period of rest. The duration of a feeding on mountain tundra pasture was shorter (70 to 80 minutes) than on forest pastures. When grazing on forest pastures, it was observed that deer spent long spells of time standing (about 10% of the 24-hour period), whereas on mountain tundra the time spent in standing amounted to about 2% of the 24-hour period.

Discussion

In analyzing the muscular activity of reindeer in wintertime as dependent on the various conditions of snowcover, it is necessary to take note of the extremely low nutritive value of the food, mostly lichens, and the resultant necessity to conserve energy during motor activity. This may account for the observation that the time spent in digging up snow and on moving about in winter is one half to one third that spent moving from place to place during summer pasturage. An important factor in reducing energy expenditure on motion in loose, deep snow must be the utilization of tracks and trails made by other deer. Another very important factor aiding energy conservation during the treks in search of food is the relative abundance of reindeer moss per unit area of winter pastures in comparison with green vegetation on summer pastures. On good sections of reindeer moss pastures, an individual adult deer can find sustenance for 24 hours within 100 - 200 m². However, under herd conditions the 24-hour pasturage area per deer is 3 to 5 times larger. Apparently this requirement for a larger area may also be explained by the necessity to maintain prolonged capacity for physical exertion under the difficult foraging conditions.

The alternation of limbs during digging should, undoubtedly, be explained from the standpoint of Sechenov's theory of "active rest". According to this view, the work capacity of a tired limb is greater if during the period of that limb's rest, work is being done by the other limb. To obtain the effect of restoration of capacity to do work in a fatigued limb, a certain degree of muscular tension in the other limb is required

(Trakhtenberg, 1955; Chakhnashvili, 1956; Krapiventseva, 1957; Muravov, 1957; Liberman, 1958, and others), that is, this effect appears when there is optimum excitation of the proprioceptors of the limb not yet performing work.

When deer dig up various types of snowcover, a certain state of muscular tension is developed, built up by the dynamic work of digging to which is added static load during eating. Since digging in hard, dense snow on mountain-tundra pastures was accompanied by a less frequent alternation of limbs than during digging up deep, loose snow, the exertion of digging under the snow on forest pastures must be considered more fatiguing. This, in spite of the fact that digging up hard snow requires the application of greater force. Further evidence that digging shallow, hard, dense snow produces less fatigue is that it is performed predominantly with the right limb, which is not the case when digging deep, loose snow. Static load on the forelimbs in extracting food from a deep hole is considerable; furthermore, deer are forced to raise their limbs to an appreciable height when digging deeply. Under these conditions of deep, loose snow, the short duration of digging (normally 5 to 15 minutes) from one hole and alternation of this activity when moving over snow-covered ground may be regarded as supplementary and necessary mechanisms for the high level maintenance of the prolonged capacity to work as fatigue develops. The work of digging deep, loose snow is therefore more fatiguing and involves a considerably higher expenditure of time standing at rest.

According to data obtained by Vereshchagin (1957) and Muravov (1957), the "active rest" effect is more markedly expressed during static efforts than during dynamic exertions. In this connection it is of interest to point out that deer often hold one of the forelimbs in a semi-bent position, increasing the static load on the opposite limb. With a switch from digging one type of snowcover to another, the functioning of neuromuscular groups is readjusted to a new level. During the first stage of adjustment, the energy expenditure on work inevitably increases, since muscles not previously employed are activated. During muscular activity, the rhythm and force of digging motions change, resulting in energy conservation, prevention of fatigue, and the preservation of prolonged capacity for physical exertion. Changes of the rhythm of the digging motions, which depend on the kind of snowcover, are interesting in the light of the theory of Ukhtomskii with respect to rhythmic adaptation. It is possible that in the process of rhythmic adaptation, more economical expenditure of energy is brought about in food procurement.

The more rapid decrease of work-capacity in digging deep, loose snow on forest pastures is no indication of an increased energy expenditure on extracting food from under the snow, in comparison with digging up snow on mountain-tundra pastures. Since there is no substantial difference in nutritive value of these two types of pastures (Makhaeva, 1959), evidence of a considerably greater expenditure of energy in digging dense, hard snow on mountainous tundras is afforded by the rapid weight loss of deer there, which averaged 320 g per 24 hours. When they grazed on forest pastures, the average 24-hour weight loss was 60 g. Use of mountain tundra pastures later in the year (May), when thawed patches appear on pastures and hardness of the snow decreases, decreased the muscular activity in digging, but treks doubled. At that period the daily weight loss was only 50 g.

Conclusions

1. The mode of muscular activity of reindeer in winter is conditioned to a considerable degree by the depth and physicomechanical properties of the snow. Digging deep, loose snow is accompanied by greater fatigue than digging shallow, hard, dense snow.

2. Under inclement conditions for digging for food (appearance of frozen snowcrust on the surface of deep, loose snow), fatigue developed faster, as expressed in shorter work periods and the reduction of the daily period devoted to foraging.

3. More rapid development of fatigue when digging deep, loose snow on forest pastures, as compared to mountainous tundra, is not indicative of increased energy expenditure in obtaining food, as evidenced by a considerably lower weight loss in the absence of substantial nutritive differences of the two types of pasture.

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